

A right hemisphere advantage at early cortical stages of processing alphanumeric stimuli. Evidence from electrophysiology



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ARTICLE INFO

Article history:

Received 1 June 2016

Revised 10 January 2017

Accepted 11 January 2017

Keywords:

RSVP

Hemispheric asymmetry

Right hemisphere advantage

Visual evoked potentials

Perceptibility hypothesis

Attentional bias

ABSTRACT

This study investigates hemispheric asymmetry evoked by non-target alphanumeric stimuli in a bilateral rapid serial visual presentation (RSVP) task. Our indicators of asymmetry are shorter latencies and larger amplitudes of the right hemisphere (RH) P1 and N1 components of visual evoked potentials (VEPs). This VEP asymmetry might reflect either a RH advantage, possibly in early perceptual processing, or for familiar stimuli, or for directing attention, or might be a paradoxical reflection of left hemisphere specialization in letter processing. Experiment 1 showed that the VEP asymmetry decreased, though remained present, with unfamiliar stimuli (Tibetan letters), as compared to familiar stimuli (Latin letters and Arabic digits). Experiment 2 showed that while leftward and rightward attentional biases affected the relation between hemispheres contra- and ipsilateral to attended visual fields, the VEP asymmetry remained independent of attention. As the most parsimonious explanation, the primary cause of the VEP asymmetry seems to be a general predominance of the RH in early perceptual processing.

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1. Introduction

Processing of written words and letters is lateralized to the left hemisphere (LH) (Dehaene & Cohen, 2011; Dien, 2009). However, recent electrophysiological studies using a bilateral rapid serial visual presentation (RSVP) task (Verleger, Dittmer, & Śmigasiewicz, 2013; Verleger, Śmigasiewicz, & Möller, 2011) suggest that the initial processing of letters may be more efficient in the right hemisphere (RH). The bilateral RSVP task consists of two streams of letters (distractor stimuli) presented with rapid succession (~130 ms per stimulus pair) simultaneously in the left and right visual fields (LVF & RVF). Two targets, T1 (a red letter) and T2 (a black digit), are embedded in those distractor streams, but at least five distractor pairs always precede the first target. The P1 and N1 components of the consecutive visual evoked potentials (VEPs) evoked by these series of pre-target distractors had shorter latencies and tended to have larger amplitudes in the RH than in the LH (Verleger, Śmigasiewicz et al., 2011; Verleger et al., 2013). No such asymmetries were found when single pairs of bilateral stimuli were presented to healthy participants (van der Lubbe & Verleger, 2002; Verleger, Binkowski, Friedrich,

Sedlmeier, & Kömpf, 2011). This asymmetry in latencies and amplitudes of RSVP-evoked VEPs might reflect a RH advantage either when perception is difficult or when stimuli are familiar or when attention has to be sustained. Alternatively, this RH speeding and increase of VEP latencies might not indicate an advantage of the RH but, paradoxically, of the LH. These four hypotheses are detailed in the following paragraphs.

1.1. RH advantage in early perceptual processing

The RH may generally be more efficient than the LH at early cortical stages of visual information processing (Grabowska & Nowicka, 1996; Hellige & Webster, 1979). This hypothesis, called the stimulus perceptibility hypothesis (Hellige & Michimata 1989), states that the RH is better equipped to perform initial perceptual operations on visual information, regardless of other hemispheric specializations at later, cognitive stages. However, this advantage becomes evident only when perceptual demands are high enough, e.g., when stimuli are presented with short exposure duration, large retinal eccentricity, low contrast, blurred contours, etc. In such cases, performance of the RH usually suffers less than of the LH. In consequence, a left visual field (LVF) advantage may be observed even with stimuli for which the LH is dominant, like gratings with high spatial frequencies or letters and words (Grabowska, Nowicka, & Szatkowska, 1992; Hellige, 1980; Hellige

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& Michimata 1989; Hellige & Webster, 1979; Jonsson & Hellige, 1986; Polich, 1978; Sergent, 1983; for review see: Christman, 1989; Grabowska & Nowicka, 1996). This criterion of high perceptual demands may also apply to the stimuli in the bilateral RSVP task by their being presented briefly, laterally, and in rapid series. The VEP asymmetry may therefore reflect the RH advantage in early perceptual processing.

1.2. RH advantage in processing familiar stimuli

In the RSVP studies reporting the VEP asymmetry (Verleger et al., 2011, 2013) only Latin letters were used as distractor stimuli, which were very familiar to participants. Studies on stimulus familiarity have shown that “our perceptual system is organized around familiar events and perception is most efficient with these learned events” (Bülthoff & Newell, 2006, p.315). Accordingly, the visual N170 component of event-related potentials (ERP) was found to be enhanced with well-known, familiar stimuli, like Latin letters for English readers (Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013; Wong, Gauthier, Woroch, DeBuse, & Curran, 2005), bird and dog pictures for experts in these domains (Tanaka & Curran, 2001), or musical scores for musicians (Proverbio, Manfredi, Zani, & Adorni, 2013). Of importance, increased familiarity may affect the functional inter-hemispheric organization of visual perception: LVF/RH perceptual biases for familiar stimuli have been observed in humans (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Laeng, Shah, & Kosslyn, 1999) and even in non-human animals, like dolphins (Blois-Heulin, Crével, Böye, & Lemasson, 2012). Thus, the VEP asymmetry may reflect such RH advantage in processing of familiar stimuli.

1.3. LVF bias in shifting attention

The VEP asymmetry might also result from attentional bias to the LVF. The premise for such an account is that the RH is more efficient in some aspects of attention (Mesulam, 1999; Shulman & Corbetta, 2012). In this line, a LVF bias has been observed in healthy people (Asanowicz, Marzecová, Jaśkowski, & Wolski, 2012; Du & Abrams, 2010; Siman-Tov et al., 2007) and a spatial neglect of the LVF is often present in patients with RH injuries (Bartolomeo, 2014; Corbetta & Shulman, 2011). Moreover, in the bilateral RSVP task as used in the present study, the second target (T2) is identified with a consistent LVF advantage (Asanowicz, Śmigasiewicz, & Verleger, 2013; Holländer, Corballis, & Hamm, 2005; Verleger et al., 2009; Verleger et al., 2011; Verleger et al., 2013; Śmigasiewicz et al., 2010), which is probably caused by the RH advantage in orienting of attention (Śmigasiewicz, Asanowicz, Westphal, & Verleger, 2015; Śmigasiewicz, Hasan, & Verleger, 2017; see Verleger & Śmigasiewicz, 2015, for review).

1.4. LH specialization in letter processing

LH specialization in word and letter processing is a well-established fact (Dehaene & Cohen, 2011; Dien, 2009). Therefore, the consistently found asymmetry, apparently indicating a RH advantage, might actually be related to that LH specialization. To detail, it might be that VEPs are delayed in the LH because it is the LH that has to do the job of identifying the letters while the RH gets finished earlier with its simpler task of globally processing the sensory stimulation from the LVF and transmitting this stimulation to the LH for further processing.

1.5. Present experiments

In order to distinguish between these hypotheses, two experiments were conducted. In Experiment 1, the question was exam-

ined whether the VEP asymmetry in the bilateral RSVP task is a general phenomenon or is related to the stimulus material. We compared VEPs evoked by Latin letters (as always used before in this task) with VEPs evoked by two different types of distractor stimuli, Arabic digits and Tibetan letters. According to perceptibility hypothesis, the VEP asymmetry reflects a general advantage of the RH in perceptual processing, thus all distractor types should evoke earlier and larger VEPs at the RH than at the LH. According to familiarity hypothesis, familiar distractors (Latin letters and Arabic digits) will evoke larger VEP asymmetry than Tibetan letters (unknown to our participants). According to LH specialization hypothesis, Latin letters will evoke earlier and larger VEPs at the RH than the LH, while Tibetan letters will not. The status of digits is somewhat unclear under this hypothesis. Digits, being alphanumeric stimuli like letters, might be preferentially processed in the LH (cf. Dien, 2009). However, recent ERPs and fMRI studies have shown that digits are preferentially processed in the RH's visual system (Park, Chiang, Brannon, & Woldorff, 2014; Park, Hebrank, Polk, & Park, 2012; see also Shum et al., 2013). If this applies here too, the specialization hypothesis predicts a reversal of asymmetry with digits: earlier and larger VEPs at the LH rather than at the RH. It is also worth mentioning that the predictions of familiarity and specialization hypotheses on the effects of Tibetan letters are in line with a recent fMRI study showing that Chinese letters (unknown to participants) evoke symmetrical, object-like activations in occipito-temporal areas of visual areas of both hemispheres (Szwed, Qiao, Jobert, Dehaene, & Cohen, 2014).

In Experiment 2, we induced attentional biases to LVF and RVF and compared their effects on VEP asymmetry. While the two streams of distractor stimuli (Latin letters) were presented simultaneously in left and right VFs (as usual and like in Experiment 1), the two targets, T1 and T2, were presented only in one VF, left or right (block-wise). Participants were instructed to focus covert attention on the “target VF” from the beginning of each trial, while keeping central fixation (controlled with an eye-tracker). According to perceptibility hypothesis, VEPs should be evoked earlier and have larger amplitude at the RH than at the LH regardless of whether attention is directed to the RVF or LVF. According to attentional bias hypothesis, with leftward bias of attention VEPs should be evoked earlier and be larger at the RH than at the LH, whereas with rightward bias of attention VEPs should be evoked earlier and be larger at the LH than at the RH.

The behavioral measure in this paradigm is the accuracy in identifying T1 and T2. These results are provided briefly in an Appendix, because processes related to target identification are beyond the scope of this study. The Appendix also includes correlations between VEP asymmetry and the asymmetry in accuracy of the identification of LVF and RVF targets. As mentioned before, T2 is identified with a LVF advantage, but the relationship between this VF asymmetry in target identification and the pre-target VEP asymmetry is unclear, especially since the first target, T1, is identified equally well in both VFs (Verleger et al., 2009, 2011) or even with some RVF advantage (Śmigasiewicz et al., 2010).

2. Experiment 1

2.1. Method

2.1.1. Participants

Data from fifty-five right-handed students (35 females and 20 males) of the University of Lübeck were analyzed. Their average age was 23.6 (SD = 3.2). Mean Edinburgh Inventory (Oldfield, 1971) score was 94.0 (SD 11.5). There were 18 participants in the Latin letters group, 20 in the Tibetan letters group, and 17 in the Arabic digits group. The groups did not differ in their handedness

scores, $F < 1.0$, n.s., and gender distribution, $H = 2.5$, n.s. All participants had normal or corrected-to-normal vision, reported normal color vision, and no history of neurological disorders. Informed written consent was obtained before the experiment, and 7 € were paid per hour.

The sample was selected from a data set of 86 participants, collected in three separate experiments originally aimed to explore the mechanism underlying the LVF advantage in T2 identification (see Section 2.1.3 for further procedural details). Because the basic VEP asymmetry is very small (see Results) and was varied and tested as between-subject differences, the inclusion criteria were rather conservative (see Section 2.1.4 for details). Data of twenty-eight participants were not included¹ either because P1 and N1 peaks could not be reliably measured anymore from the second pair of stimuli onwards due to habituation, or noisy EEG signal, and/or because systematic eye movements occurred toward one RSVP stream (see EEG data processing for details). Besides, three participants were not included due to high error rates in identifying T1, exceeding 2 SDs of the whole group.

2.1.2. Stimuli and apparatus

The task is illustrated in Fig. 1. Two simultaneous streams of stimuli were presented in the left and right visual field, with the two targets, T1 and T2, embedded in the streams. The targets were present and had to be identified in each trial. Distractor stimuli could be one of the three types: Latin letters (of a set of 18), Arabic digits (from 1 to 9), and Tibetan letters (e.g., སྐ, ལ, ཨ, ས, ས; of a set of 15). Each target set consisted of 6 stimuli. In the task with Latin letters, T1 was a red Latin letter (D, F, G, J, K, or L) and T2 was a black Arabic digit (ranging from 1 to 6). In the task with Arabic digits, T1 was a red Arabic digit (1–6) and T2 was a black Latin letter (D, F, G, J, K, L). Thus the task was “a mirror image” of the first one. Finally, in the task with Tibetan letters, T1 was a red Tibetan letter (སྐ, ལ, ཨ, ས, ས) and T2 was a black Arabic digit for half of participants (1–6, as in the first task) or a black Latin letter for the other half (D, F, G, J, K, or L, as in the task with Arabic digits)². Distractor stimuli, T2s (1 cd/m²) and red T1s (24 cd/m²) were presented on the white background (120 cd/m²) of a 17" screen driven with 100 Hz, at about 1.1 m from participants' eyes. The font *Helvetica* was used for letters and digits, and the font *Ü-chan* for Tibetan letters. Fixation was marked by a small red cross (0.1°, 0.1°) at the center of the screen. Stimuli were about 8.5 mm wide and 11 mm high (0.5°, 0.6°) with their inner edge about 10 mm from fixation (0.5°). Presentation® software was used for experimental control (Neurobehavioral Systems Inc., Albany, CA).

2.1.3. Procedure

Each trial started with a fixation period of 800 ms followed by a presentation of 12–20 subsequent pairs of stimuli. Participants received the instruction to keep central fixation throughout the whole trial, until the onset of the response screen. Each pair of stimuli was presented for 130 ms, immediately followed by the next frame, without inter-stimulus intervals. The fixation point was present on the screen throughout the whole trial. T1 was preceded by five, seven, or nine pairs of distractors, and could occur either in the LVF or RVF (50/50%), thus participants did not know when and where it would occur. To ensure similar temporal and spatial uncertainty of the second target, T2 occurred either on the same side as T1 or on the opposite side (50/50%), and with T1–T2 lags of 130 ms (lag 1), 390 ms (lag 3), or 650 ms (lag 5). T2 was always followed by five stimulus pairs. Therefore, trial

length varied between 12 frames (when T1 came at the 6th position and T1–T2 lag was 1) and 20 frames (when T1 came at the 10th position and T1–T2 lag was 5). Targets were randomly selected from the target sets and distractor stimuli were randomly selected with replacement. At the end of each trial, first a T1 and then a T2 response screen appeared, displaying all six possible targets and the instruction to press the appropriate key on the computer keyboard. The next trial started immediately after the response on T2. A few practice trials with stimuli presented in slow motion (500 ms display time for each pair) were performed before the proper task. The task consisted of 720 trials and lasted up to one hour and fifteen minutes.

As mentioned in the Participants section, the data were collected across three separate experiments. All of them were conducted in the same lab (Lübeck, Germany), with the same procedure and stimulus parameters (except the manipulations listed above), and with the same software and apparatus. The present analyses include data of participants from the experiment with Latin letters as distractor stimuli reported in Verleger et al. (2011). The other data have not been published before. All data were reprocessed and reanalyzed for the purpose of the present study.

2.1.4. EEG data processing and analysis

EEG was recorded with Ag/AgCl electrodes (Easycap, www.easycap.de) from 60 scalp sites, including 8 midline positions from AFz to Oz and 26 pairs of symmetric left and right sites. On-line reference was Fz, data were off-line re-referenced to the nose-tip. The ground electrode was placed at Fpz. For artifact control, vertical electro-oculogram (EOG) was recorded from above vs. below the right eye, and horizontal EOG (hEOG) from positions next to the outer rims of the eyes. Data were amplified from DC to 250 Hz by a BrainAmp MR plus (BrainProducts GmbH, Gilching, Germany) and stored at 500 Hz per channel.

Further processing was done with Brain Vision Analyzer software (ver.2, BrainProducts GmbH). Data from each trial were re-referenced, low-pass filtered at 20 Hz, and split into segments for VEP analysis. The segments spanned 900 ms, from 100 ms before the onset of the first stimulus pair to 800 ms afterwards. Segmented data were referred to the first 100 ms of the segment as baseline, and edited for artifacts, by rejecting trials with zero lines, with overall minimum-maximum voltage differences ≥ 200 μ V, with voltage steps between adjacent data points ≥ 50 μ V, and with absolute amplitudes ≥ 100 μ V. These artifact criteria removed also the segments with blinks and large eye movements. To reject any further eye movement artifacts, averages of left-right side differences were calculated for horizontal EOG waveforms. Any participant's data were rejected if these averages deviated from baseline by 8 μ V, as an indication of eye movements $\geq 0.6^\circ$ toward the left or right RSVP stream. Finally, data were high-pass filtered at 3 Hz to exclude any artifacts from slow fluctuations (caused either by expectancy-related negativities or by random fluctuations) on our cross-correlation measure (see below). The segments were averaged over trials irrespective of locations, time-points, and identification accuracy of T1 and T2 (cf. Verleger et al., 2011, 2013). The overall average of accepted segments was 621 (SD = 99, with the minimum above 400 for all participants except two with 367 and 195 accepted trials³).

The average waveforms consisted of a series of P1–N1 deflections, evoked in intervals of 130 ms by the series of distractor stimuli. The parameter of most interest was the difference between recording sites at the scalp above right and left occipito-temporal cortex. Analyses started at the VEPs evoked by the 1st pair of stim-

¹ This is about 33% of the whole sample. Still, it is not particularly exceptional for this type of task (cf. Kranczioch, Debener, & Engel, 2003; Tan & Wyble, 2015).

² This allowed for the additional check if there were any specific interactions between T2 type and VEP asymmetry, and no such effects were found.

³ Exclusion of these two participants did not change the results.

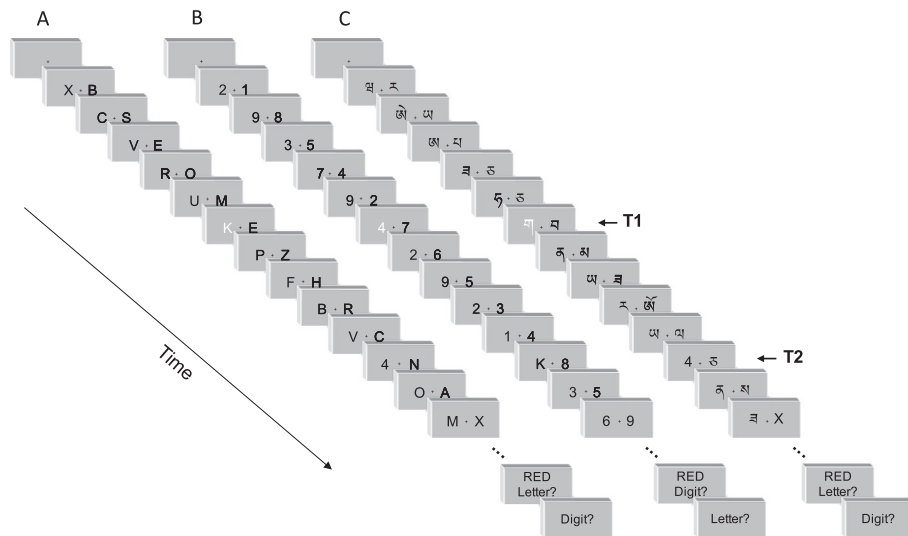


Fig. 1. Examples of the task and stimuli used in Experiment 1: (A) a trial with Latin letters as distractors, red letter T1 at the sixth pair of stimuli, and Arabic digit T2 at the lag 5 position; (B) a trial with Arabic digits as distractors, red digit T1, and Latin letter T2; (C) a trial with Tibetan letters as distractors, red Tibetan letter T1, and Arabic digit T2. Color red is replaced here by white. See Section 2.1 for details.

uli and stopped at the 5th one, because the 6th wave could already be evoked by T1.

To determine the hemispheric differences of the VEPs, first, latencies and amplitudes of the P1 and N1 peaks evoked by the first five pairs of distractor stimuli were measured as most positive peak 50–150 ms and most negative peak 140–240 ms after stimulation onset (detected semi-automatically at the sites PO7 and PO8, where VEPs were largest, and corrected manually when peaks occurred outside of these time-windows), and were submitted to ANOVAs with Hemisphere (PO7, PO8) and Serial Position (1st, 2nd, 3rd, 4th, and 5th pair of stimuli) as within-subject factors, and Stimulus Type (Latin letters, Arabic digits, Tibetan letters) as between-subject factor. Second, a cross-correlation method was employed to determine latency differences between the hemispheres across the entire length of the VEP waveforms (Okon-Singer et al., 2011; Verleger et al., 2013). The difference was determined by shifting each participant's waveforms of 800 ms duration (which included the first five VEPs) from left sites against their symmetric right sites in 2 ms steps within ± 50 ms, and selecting the lag at which the cross-correlation was largest. Latency shifts were tested against zero, and were submitted to one-way ANOVA with the factor Stimulus Type (Latin letters, Arabic digits, Tibetan letters).

As it turned out, these planned analyses did not reveal the interaction predicted by familiarity hypothesis between Hemisphere and Stimulus Type (see Results). Yet inspection of waveforms suggested that the hemisphere effect may in fact be smaller with the unfamiliar Tibetan letters than with the familiar Latin letters and Arabic digits. Therefore, we performed an additional, *post hoc* analysis to further test this hypothesis. The RH minus LH (PO8–PO7) difference waveforms (Figs. 2 and 5) showed periodic positive and negative maxima, about 25 ms before P1 and about 50 ms before N1. These maxima provided convenient measures of the composite effect of latency and amplitude differences between hemispheres: The positive maximum was formed by PO8 potentials being earlier and being more positive than PO7 potentials on their way to positivity, and the negative maximum was formed by PO8 potentials being earlier and being more negative than PO7 potentials on their way to negativity. The maxima were measured semi-automatically as most positive peak 40–150 ms and most negative peak 120–240 ms after stimulation onset in the PO8–PO7 difference waves,

separately for each participant. Next, the amplitudes of these maxima were then tested against zero, as indices of hemispheric asymmetry, and submitted to ANOVAs, separately for positive and negative maxima, with Serial Position (1st–5th pair of stimuli) as within-subject factors, and Stimulus Type (Latin letters, Arabic digits, Tibetan letters) as between-subject factor.

Degrees of freedom were corrected in all analyses by Greenhouse–Geisser's ϵ when repeated-measure factors had three or more levels (i.e., for Serial Position).

2.2. Results

Grand-average waveforms of the first 800 ms of each trial recorded at the PO7 and PO8 sites are depicted in Fig. 2, separately for the three distractor stimulus types, along with the PO8–PO7 difference waves, and with topography maps for each of the first five P1 and N1 peaks. The three stimulus types are directly compared to each other in Fig. 3. Mean latencies and amplitudes of the P1 and N1 peaks are plotted in Fig. 4.

2.2.1. VEP latencies

2.2.1.1. P1 latencies. P1 peaked on average 5 ms earlier at the RH than at the LH (120 vs. 125 ms), $F_{1,52} = 23.3$, $p < 0.001$. Importantly, this asymmetry was not affected by Stimulus Type, nor was it modified by Serial Position, $F_s < 1.0$. Irrespective of asymmetry, P1 latencies were shortest with Latin letters (116 ms), intermediate with digits (124 ms) and longest with Tibetan letters (128 ms) (Stimulus Type: $F_{2,52} = 4.1$, $p = 0.022$, Latin letters vs. digits: $F_{1,33} = 3.3$, $p = 0.08$, Latin vs. Tibetan letters: $F_{1,36} = 7.5$, $p = 0.009$, digits vs. Tibetan letters: $F_{1,35} = 1.1$, $p = 0.30$). The main effect of Serial Position, $F_{4,208} = 28.4$, $p < 0.001$, reflects a quadratic trend, $F = 63.1$, with longest latencies at the 3rd position, and the Stimulus Type effect was most pronounced at the 3rd position (Serial Position \times Stimulus Type: $F_{8,208} = 2.9$, $p = 0.008$). Besides, as can be seen on Figs. 3 and 4 the difference between Latin and Tibetan letters was relatively stable across the serial positions (and remained significant even when calculated without the 3rd position, $F = 4.5$, $p = 0.04$), whereas digits fell in between the two types of letters.

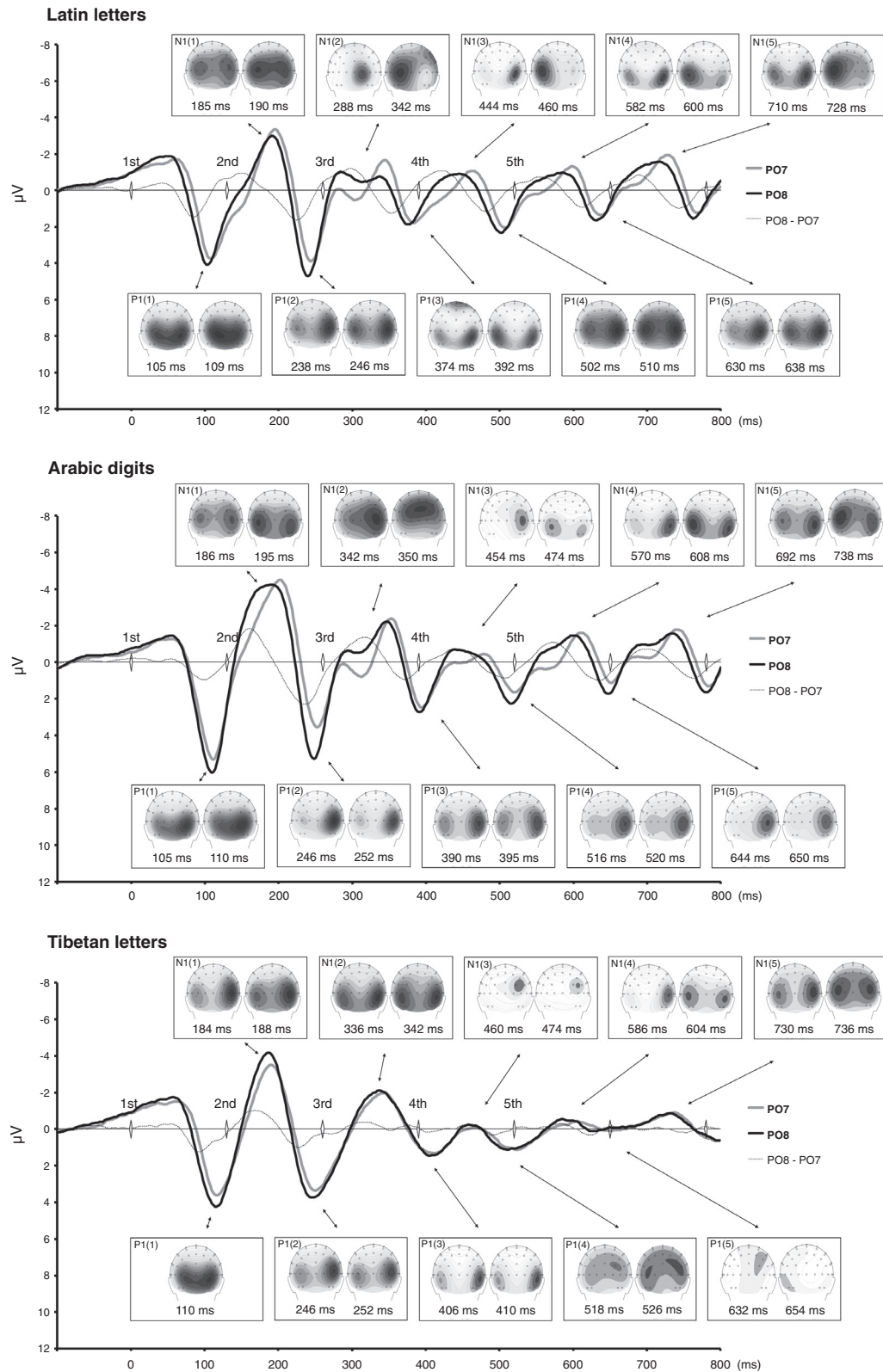


Fig. 2. Experiment 1. P1 and N1 potentials evoked by the two lateral RSVP streams during the first 800 ms of trials with the three types of stimuli: Latin letters (upper panel), Arabic digits (middle panel), and Tibetan letters (bottom panel). The solid black and grey waveforms are grand means recorded from PO7 and PO8 (above the right and left visual cortex), starting 100 ms before onset of the first pair of the stimulus series. The thin dotted line shows the PO8-PO7 difference. Negative voltage points upwards. Time-point zero is onset of the first stimulus pair. The following marks on the zero-line horizontal axes denote the onsets of the subsequent four stimulus pairs (at 130, 260, 390, and 520 ms). Only potentials evoked by the first five pairs were analyzed (as the 6th pair can already include T1). The head maps depict topographies of the five consecutive P1s (on the bottom of each panel) and N1s (at the top of each panel) evoked by the first five pairs of the stimulus series. The head view is from the back. The maps are min-max scaled, with both ends of the scale in dark grey and zero voltage in white. As the peak latencies may differ between hemispheres, two time points are presented for each potential, one for the peak at PO8 (which is generally earlier) and the second for the peak at PO7. Only one map is presented for the first P1 evoked by Tibetan letters (bottom panel) because there was no latency difference between PO7 and PO8 in this case.

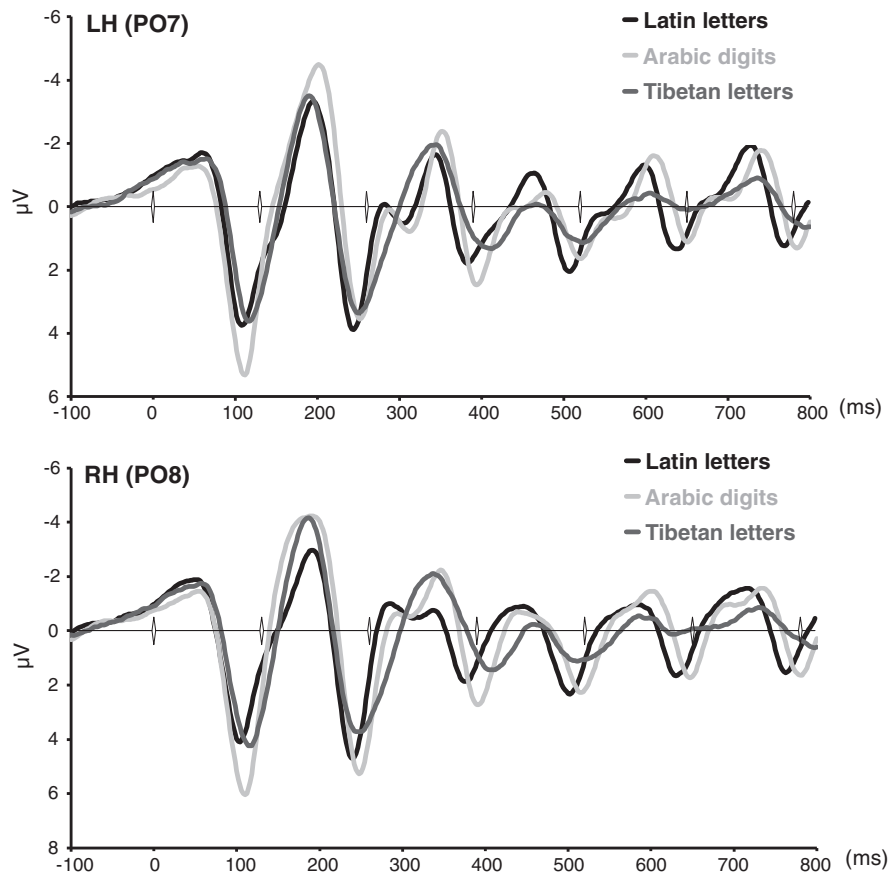


Fig. 3. Experiment 1. This figure presents the same waveforms as Fig. 2, but in a way that allows comparisons between the three types of stimuli, Latin letters (black lines), Arabic Digits (light grey lines), and Tibetan letters (dark grey lines), separately for LH (PO7, upper panel) and RH (PO8, bottom panel). Negative voltage points upwards. Time-point zero is onset of the first stimulus pair. The following marks on the horizontal zero lines denote the time-points of the subsequent stimulus pair onset (at 130, 260, 390, and 520 ms).

2.2.1.2. N1 latencies. N1 peaked 8 ms earlier at the RH than at the LH (193 vs. 201 ms), $F_{1,52} = 37.8$, $p < 0.001$, and, importantly, this asymmetry, again, was not significantly affected by Stimulus Type and Serial Position, $F \leq 2.4$, $p \geq 0.10$. N1 latencies were generally shortest with Latin letters (190 ms), as compared with digits (202 ms) and Tibetan letters (200 ms) (Stimulus Type: $F_{2,52} = 2.9$, $p = 0.06$, Latin letters vs. digits: $F_{1,33} = 4.5$, $p = 0.042$, Latin vs. Tibetan letters: $F_{1,36} = 5.0$, $p = 0.031$, digits vs. Tibetan letters: $F < 1.0$, n. s.). Latencies slightly increased from the 1st position onwards (Serial Position: $F_{4,208} = 5.0$, $p = 0.001$), though somewhat differently for each stimulus (Stimulus Type \times Serial Position: $F_{8,208} = 2.9$, $p = 0.006$), such that differences between Latin and Tibetan letters were well pronounced from the 2nd position onwards, while with digits latencies tended to be longest except for the 3rd position (see Fig. 4).

2.2.1.3. Cross-correlation of the entire 800 ms epoch. Maximum correlation between the LH (PO7) and RH (PO8) waveforms was found when the RH waveforms were shifted to lead by 4 ms. This lag was significantly larger than zero, $t_{54} = 6.6$, $p < 0.001$, and did not differ significantly between the three types of stimuli, $F_{2,52} < 1.0$. (Latin letters: 4.7 ms, Arabic digits: 3.3 ms, Tibetan letters: 4.0 ms).

2.2.2. VEP amplitudes

2.2.2.1. P1 amplitudes. P1 amplitudes were reduced from the 2nd position onwards (Serial Position: $F_{4,208} = 69.8$, $p < 0.001$, linear trend: $F = 316.8$), and were larger at the RH than at the LH (Hemisphere: $F_{1,52} = 13.4$, $p = 0.001$). This asymmetry was larger at the first two positions than at the three later positions, Hemisphere \times Serial Position $F_{4,208} = 3.6$, $p = 0.022$, but remained significant when testing only the 3rd, 4th, and 5th positions, $F_{1,52} = 10.3$, $p = 0.002$. Importantly, Stimulus Type did not affect the Hemisphere effect, $F < 1.0$. The effect of Stimulus Type was significant, $F_{2,52} = 5.0$, $p = 0.010$: P1 amplitudes were smallest for Tibetan letters and largest for digits (Latin letters vs. digits: $F_{1,33} = 1.9$, $p = 0.17$, Latin vs. Tibetan letters: $F_{1,36} = 3.0$, $p = 0.091$, digits vs. Tibetan letters: $F_{1,35} = 10.6$, $p = 0.003$).

2.2.2.2. N1 amplitudes. The main effect of Serial Position, $F_{4,208} = 67.8$, $p < 0.001$ reflected a quadratic trend, $F = 96.6$, with N1 amplitudes being largest at the 1st position, then getting reduced until the 3rd position and then slightly recovering until the last position. The Hemisphere effect was not significant, $F_{1,52} = 2.6$, $p = 0.11$, and did not interact with any factor, $F \leq 1.3$, n.s. The Stimulus Type effect was significant, $F_{2,52} = 6.5$, $p = 0.003$. N1 amplitudes were smallest for Tibetan letters and largest for digits (Latin letters vs. digits: $F_{1,33} = 4.0$, $p = 0.05$, Latin vs. Tibetan letters: $F_{1,36} = 2.7$, $p = 0.11$, digits vs. Tibetan letters: $F_{1,35} = 11.3$, $p = 0.002$).

2.2.3. Maxima of hemispheric differences
Grand means of the PO8-PO7 difference waveforms are displayed in Fig. 2. Amplitudes of their positive and negative maxima are displayed in Fig. 5.
Positive maxima were significantly larger than zero for each serial position, $t_{54} \geq 9.1$, $p < 0.001$, and were smaller from the 2nd position onwards (Serial Position: $F_{4,208} = 20.8$, $p < 0.001$). Importantly, these positive maxima were modulated by Stimulus

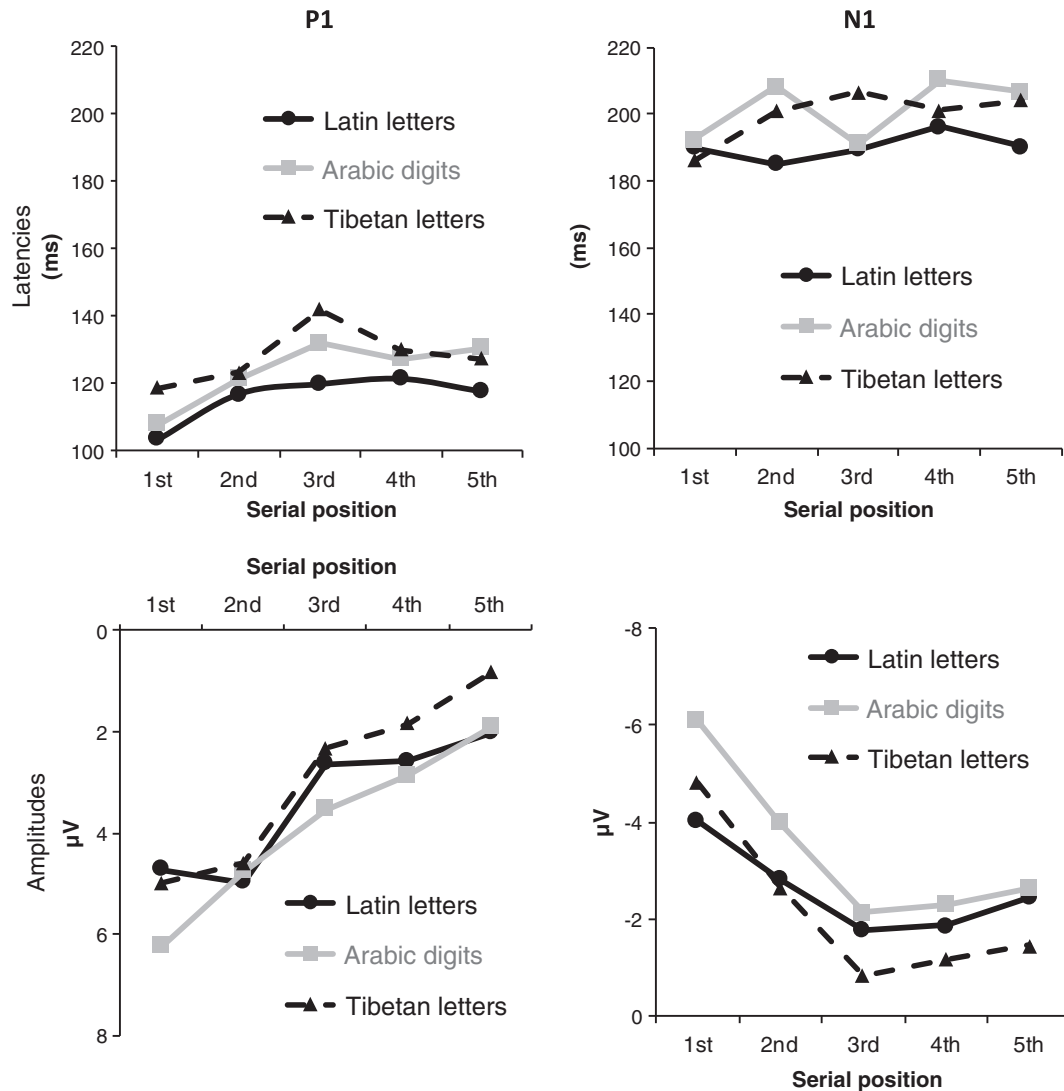


Fig. 4. Experiment 1. Mean P1 and N1 latencies and amplitudes pooled across the hemispheres for the three types of stimuli, Latin letters (black solid lines), Arabic Digits (black dashed lines), and Tibetan letters (grey solid lines).

Type, $F_{2,52} = 3.2$, $p = 0.049$. The asymmetry was smaller with Tibetan letters than with the two familiar stimulus types, though still significantly different from zero for each serial position, $t_{19} \geq 4.9$, $p < 0.001$. The Stimulus Type effect for Latin letters and Arabic digits (omitting Tibetan letters) was not significant, $F < 1.0$, indicating no difference in terms of the hemispheric asymmetry between these two types of stimuli.

Negative maxima of the PO8-PO7 difference waves were also significantly larger than zero for each serial position, $t_{54} \geq 9.4$, $p < 0.001$, and decreased from the 1st position onwards (Serial Position: $F_{4,208} = 22.6$, $p < 0.001$). Like with the positive maxima, this hemispheric difference was modulated by Stimulus Type, $F_{2,52} = 4.4$, $p = 0.016$, indicating smaller, but still significant, $t_{19} \geq 5.5$, $p < 0.001$, asymmetry with Tibetan letters than with the two familiar stimulus types. The Stimulus Type effect without Tibetan letters was again not significant, $F < 1.0$.

3. Experiment 2

3.1. Methods

Only differences from Experiment 1 will be described.

3.1.1. Participants

Twenty-one right-handed students (13 females) participated in the study. One participant had to be rejected from analysis due to systematic eye movements toward the target streams. Mean age of the remaining participants was 23.1 years ($SD = 3.1$) and their mean Edinburgh Inventory (Oldfield, 1971) score was 95.0 ($SD 7.7$).

3.1.2. Stimuli, apparatus, and procedure

The two streams of distractor stimuli (Latin letters) were presented simultaneously in the left and right visual VFs, as in the previous experiment, whereas the two targets, T1 and T2, were presented only in one VF, left or right. The target side changed block-wise, and T2 occurred always on the same side as T1. Target side in the initial block alternated between participants. For reasons not of interest to the present question, T1–T2 lags amounted to 260 ms (lag 2), 520 ms (lag 4), 780 ms (lag 6), or 1040 ms (lag 8). Thus, while participants always knew where the targets would occur, they did not know when they would occur. T2 was always followed by three stimulus pairs. Therefore, trial length varied between 11 frames (when T1 came at the 6th position and T1–T2 lag was 2) and 21 frames (when T1 came at the 10th position and T1–T2 lag was 8). The whole task consisted of 576 trials (288 per target-side condition, 144 per block). In order to facilitate

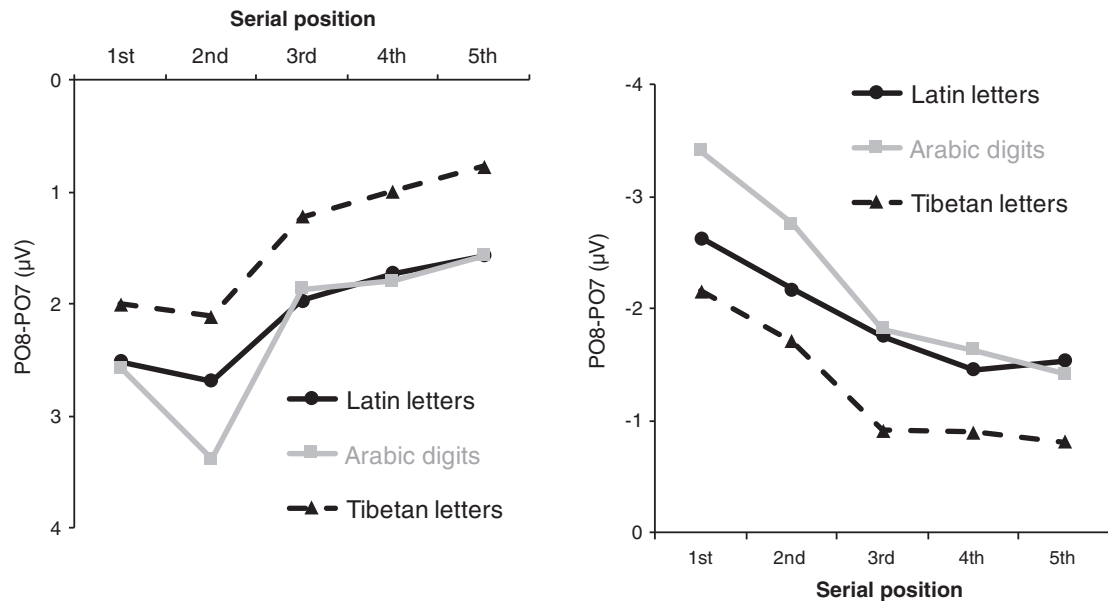


Fig. 5. Experiment 1. Mean amplitudes of the positive maxima (left panel) and negative maxima (right panel) of PO8-PO7 difference waves (see Methods of Exp.1 for details) for the three types of stimuli, Latin letters (black solid line), Arabic Digits (black dashed line), and Tibetan letters (grey solid line) across the five serial positions of the subsequent stimulus pairs.

focusing on one stream, stimuli were presented with slightly greater eccentricity than in Experiment 1, with their inner edge about 14 mm from fixation (0.7°).

Participants were carefully instructed to focus their covert attention on the “target VF” from the beginning of each trial, while keeping central fixation. They also read written instruction with an explanation of why proper fixation is important. Fixation was controlled with a remote infrared eye tracker (600 series bin-ocular; Eyegaze LC Technologies, Fairfax, VA) and online feedback by software (Interactive Minds, Dresden, Germany), which communicated with the Presentation program. In case of a deviation of more than 6 mm from vertical midline, a red exclamation mark was presented at midline, inducing shifts of gaze back to fixation.

3.1.3. Data analysis

The analyses included a within-subject factor Target Stream (contralateral vs. ipsilateral to recorded side) in addition to the previously used Hemisphere (PO7, PO8) and Serial Position (1st–5th) factors. Only trials with correct T1 identification were included into the analyses, because errors in T1 identification might indicate a lacking focus of attention on the proper VF from the beginning of a trial, i.e., a failure to cope with the key manipulation of this experiment. The overall average of VEP-segments accepted for analysis was 490 (SD = 78, range 239–566). The analysis of maxima of the PO8-PO7 difference waves turned out to be redundant and will not be reported, for brevity. Behavioral results and their correlations with VEP asymmetry will be reported in the [Appendix](#).

3.2. Results

Fig. 6 shows grand-average waveforms recorded at PO7 and PO8 sites during the first 800 ms of each trial in the LVF attention and the RVF attention conditions. The topography maps show activity for the P1 and N1 peaks evoked by the first pair of stimulus series. **Fig. 7** shows the same waveforms in different arrangement.

3.2.1. VEP latencies

3.2.1.1. P1 latencies. The ANOVA showed significant main effects of Serial Position, $F_{4,76} = 6.6$, $p = 0.002$, and, importantly, of Hemisphere, $F_{1,19} = 8.8$, $p = 0.008$, and of Target Stream, $F_{1,19} = 16.6$, $p = 0.001$. P1 peaked 6 ms earlier at the RH than at the LH, and 5 ms earlier with contra- than ipsilateral target streams. Since interactions were not significant, $F \leq 1.6$, the basic RH advantage was independent of attention: Effects of Hemisphere and Target Stream added when attention was focused on the LVF (making the RH lead by 11 ms, $F_{1,19} = 15.7$, $p = 0.001$) and cancelled each other when attention was focused on the RVF (yielding a non-significant difference of 1 ms between RH and LH).

3.2.1.2. N1 latencies. As with P1, the ANOVA showed significant main effects of Serial Position, $F_{4,76} = 8.6$, $p = 0.001$, and, importantly, of Hemisphere, $F_{1,19} = 15.1$, $p = 0.001$, and of Target Stream, $F_{1,19} = 6.0$, $p = 0.024$. N1 peaked 10 ms earlier at the RH than at the LH and 4 ms earlier with contra- than ipsilateral target streams. Interactions were not significant, $F \leq 2.3$. Thus, again the basic RH advantage was independent of attention. Effects of these two factors added when attention was focused on the LVF (making the RH lead by 14 ms, $F_{1,19} = 15.8$, $p = 0.001$) and cancelled each other when attention was focused on the RVF (yielding a small though still significant lead of 6 ms for RH over LH, $F_{1,19} = 6.0$, $p = 0.024$).

3.2.1.3. Cross-correlation of the entire 800 ms epoch. Maximum correlation between the LH (PO7) and RH (PO8) waveforms pooled across the two attention condition was found with the RH waveforms shifted to lead by 4.2 ms over the LH, $t_{19} = 1.9$, $p = 0.073$. When we compared the two contralateral sites (PO7 with attention to RVF vs. PO8 with attention to LVF), we found the LH to lag behind the RH by 4.5 ms, but this effect did not reach the significance level, $t_{19} = 1.7$, $p = 0.09$. Nearly the same lag was obtained on average for the ipsilateral sites (PO7 with attention to LVF vs. PO8 with attention to RVF), with the LH lagging behind the RH by 4.6 ms, which was significant, $t_{19} = 2.1$, $p = 0.049$ (cf. **Fig. 7**).

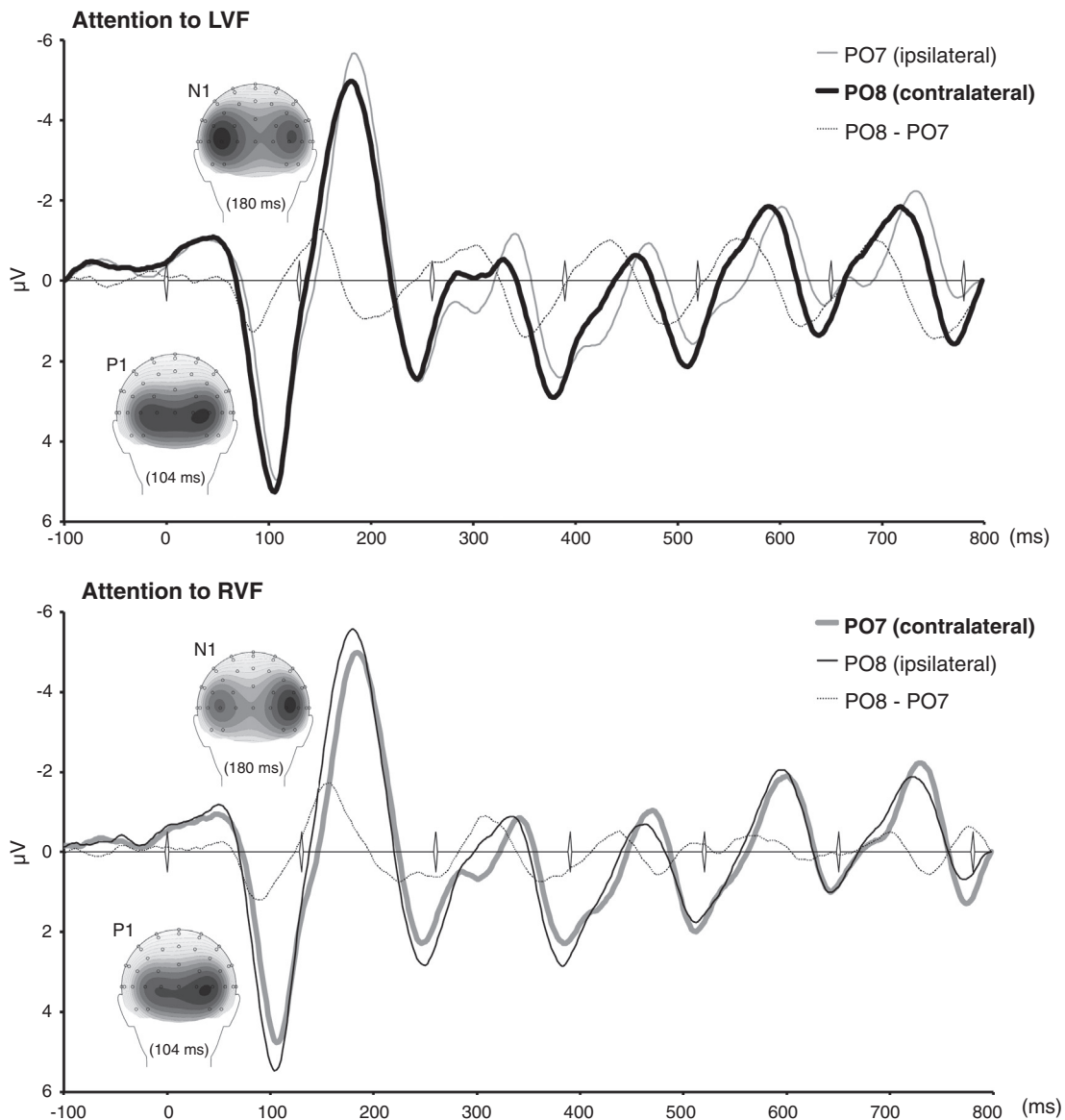


Fig. 6. Experiment 2. P1 and N1 potentials evoked during the first 800 ms of trials by the two lateralized RSVP streams of Latin letters in the two attention condition: attention to LVF (upper panel) and to RVF (bottom panel). Negative voltage points upwards. The grey and black waveforms are grand means recorded from PO7 and PO8, respectively, starting 100 ms before the onset of the first pair of the stimulus series. The bold and thin lines denote, respectively, the contralateral and ipsilateral sites (in relation to the attended VFs). Time-point zero is onset of the first stimulus pair. The following marks on the horizontal zero lines denote the time-points of the subsequent stimulus pair onset (at 130, 260, 390, and 520 ms). Only potentials evoked by the first five pairs were analyzed (as the 6th pair can already include T1). The head maps show topographies of the first P1 and N1 peaks, evoked by the first pair of the stimulus series in the attention to LVF and attention to conditions. The head view is from the back. The maps are min-max scaled, with both ends of the scale in dark grey and zero voltage in white.

The cross-correlation results are thus generally in line with the peak latency results.

3.2.2. VEP amplitudes

3.2.2.1. P1 amplitudes. The ANOVA showed significant main effect of Serial Position, $F_{4,76} = 22.6$, $p < 0.001$, and a Target Stream \times Serial Position interaction, $F_{4,76} = 8.0$, $p < 0.001$. As can be seen in Fig. 6, P1 amplitudes tended to be larger at the contralateral (right) than the ipsilateral (left) site from the 3rd position onwards when attention was focused on the LVF (Target Stream \times Serial Position for Attention to LVF: $F_{4,76} = 2.5$, $p = 0.06$; Target Stream from the 3rd position onwards for Attention to LVF: $F_{1,19} = 5.4$, $p = 0.031$). Although Fig. 6 might suggest otherwise, the differences between contra- and ipsilateral sites at the first

three positions with attention on RVF were not significant (Target Stream for the first three positions: $F = 2.6$, $p = 0.12$). Importantly, effects of Hemisphere were not significant ($F_s \leq 1.6$, cf. Fig. 7).

3.2.2.2. N1 amplitudes. Like for P1, the ANOVA yielded a main effect of Serial Position, $F_{4,76} = 37.3$, $p < 0.001$, and a Target Stream \times Serial Position interaction, $F_{4,76} = 5.0$, $p = 0.002$, resolved to a main effect of Target Stream at the 1st Serial Position, $F_{1,19} = 19.9$, $p < 0.001$ (Target Stream at the 2nd–5th positions: $F < 1.0$, n.s.; interaction of Target Stream \times Serial Position without the 1st position: $F = 1.2$, n.s.). As can be seen in Fig. 6, N1 evoked by the 1st pair of stimuli was larger when the attended VF was ipsilateral than when it was contralateral. Effects of Hemisphere were again not significant ($F_s < 1.0$, cf. Fig. 7).

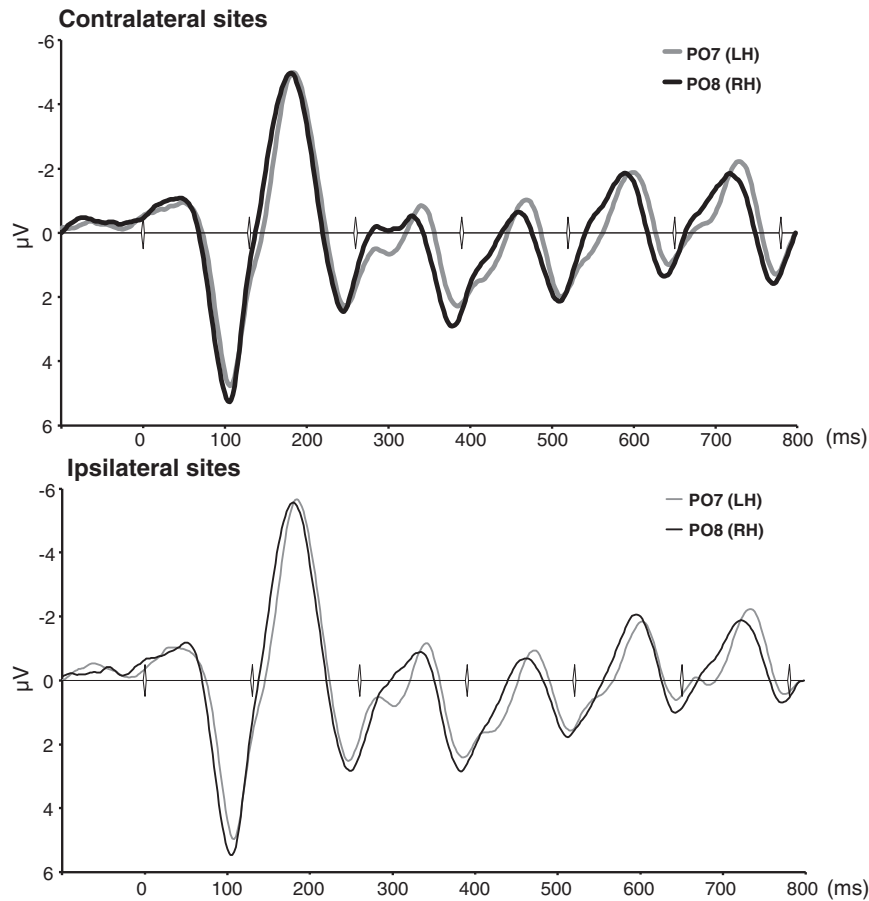


Fig. 7. Experiment 2. This figure presents the same waveforms as Fig. 6, but in a way that allows to compare the two waveforms recorded at the hemispheres contralateral to the attended VF, i.e., LH/attention to RVF vs. RH/attention to LVF (upper panel), representing processing with attention, and the two waveforms recorded at the hemispheres ipsilateral to the attended VF, i.e., LH/attention to LVF vs. RH/attention to RVF (lower panel), representing perceptual processing without attention. Negative voltage points upwards. The grey and black waveforms are grand means recorded from PO7 and PO8, respectively, starting 100 ms before the onset of the first pair of the stimulus series. The bold and thin lines denote, respectively, the contralateral and ipsilateral sites (in relation to the attended VFs). Time-point zero is onset of the first stimulus pair. The following marks on the horizontal zero lines denote the time-points of the subsequent stimulus pair onset (at 130, 260, 390, and 520 ms).

4. Discussion

4.1. Summary of results

In Experiment 1, the VEPs evoked by all three types of stimuli, Latin letters, Arabic digits, and Tibetan letters, had shorter latencies and larger amplitudes at the RH than at the LH, thereby replicating the previous findings by Verleger et al. (2011, 2013). This asymmetry was reduced with Tibetan letters, as found in the analysis of the maxima of the hemispheric difference waves, which provided composite effects of latency and amplitude differences between hemispheres. Besides, stimulus type had an overall impact on VEP amplitudes and latencies. In particular, the VEPs evoked by the unfamiliar Tibetan letters tended to have smallest amplitudes, whereas the largest amplitudes were found with Arabic digits, and the shortest latencies were obtained with Latin letters.

In Experiment 2, biasing attention to the left or right stream resulted in typical effects of attention on perceptual processing: VEP latencies were shorter at the sites contralateral to the attended VF than at the ipsilateral sites (cf. the sensory gain model of attention, Hillyard, Vogel, & Luck, 1998). Besides, the usual shorter VEP latencies at the RH than at the LH were observed, as well. Importantly, these two effects did not interact. The amplitude analysis showed smaller and less consistent effects than the latency analysis.

P1s tended to be larger at contralateral than at ipsilateral sites, but only with attention to LVF and only from the 3rd serial position onwards. Interestingly, at the 1st position, the ipsilateral N1s tended to be larger than the contralateral N1s. No differences between hemispheres were found in the VEP amplitudes.

It may be summarized that the VEP asymmetry in this RSVP task has been more consistently found in latency measures, being observed in both present experiments and in both previous studies by Verleger et al. (2011, 2013), than in amplitudes, observed only in the first of present experiments for P1s and by Verleger et al. (2013) for N1s. Thus, the asymmetry may be primarily related to the speed of processing. Still, there is a question whether the larger VEP amplitudes in the RH, when observed, reflect higher or lower efficiency. From the four present hypotheses, only the specialization hypothesis suggests unambiguously the second alternative.

4.2. Perceptibility hypothesis

According to perceptibility hypothesis, the VEP asymmetry reflects a general advantage of the RH in early perceptual processing, thus VEPs should have shorter latencies and larger amplitudes at the RH than at the LH, regardless of stimulus type and regardless of whether attention is directed to the LVF or RVF. The results showed that, although being modulated by stimulus familiarity (Exp.1) and adding to attentional biases (Exp.2), the VEP asymme-

try always remained present, at least in one VEP component and especially in processing speed, under each condition of the two experiments. These results are therefore in agreement with perceptibility hypothesis.

4.3. Familiarity hypothesis

According to familiarity hypothesis, the VEP asymmetry should be larger with familiar than unfamiliar stimuli. In accordance with this hypothesis, Experiment 1 showed that the asymmetry was smaller with unfamiliar Tibetan letters than with Latin letters and Arabic digits, as shown by analyses of the positive and especially the negative maxima of hemispheric differences. Therefore, the asymmetry in VEPs observed in previous dual RSVP experiments (Verleger et al., 2011, 2013) might be partially caused by a RH advantage in processing familiar stimuli. In this context, it might be worth noting that the N1 component is related to a discrimination process (Vogel & Luck, 2000). Possibly, stimulus familiarity is more relevant at the level of discrimination than at earlier, more basic processing stages indexed by P1. Thus, it may make sense that the familiarity effect on the VEP asymmetry was more pronounced in the later, negative components of the hemispheric difference waves.

The generally smaller amplitudes of the VEPs evoked by the unfamiliar Tibetan letters conform to the idea that preferential processing of familiar, well known stimuli can begin already at early stages of visual processing. This is in line with ERP findings of increased N170 with familiar stimuli (Proverbio et al., 2013; Tanaka & Curran, 2001; Wong et al., 2005), as well as with fMRI findings that BOLD responses specific to well-known written words can be observed already in the early visual areas from V1 to V4 (Szwed et al., 2011, 2014). It remains unclear why Arabic digits tended to evoke VEPs with largest potentials, while Latin letters tended to evoke VEPs with shortest latencies. The digit effect may be related to size of the stimulus set, which was smallest with digits (1–9) and included the largest proportion of potential T1 targets (digits 1–6). Nevertheless, considering weak consistency and statistical significance of those differences, any firm conclusions cannot be yet drawn.

4.4. Attentional bias hypothesis

Experiment 2 showed that biasing covert attention to left and right VFs modulated lateralization of the VEPs. This is in line with a large number of studies showing that attention may be able to modulate every aspect of perception at almost every stage of processing (Luck & Kappenman, 2012; Serences & Kastner, 2014, see also recent RSVP studies: Śmigajewicz, Weinrich, Reinhardt, & Verleger, 2014; Śmigajewicz et al., 2017). However, contrary to the prediction of attentional bias hypothesis, the effect of attention did not interact with hemispheric asymmetry, but was additive to it: Asymmetry was equally large between hemispheres when sites were contralateral to the attended stream and when sites were ipsilateral. Thereby, biasing attention to the RVF stream exactly balanced the hemispheric asymmetry for P1 latency and mitigated it for N1 latency. In conclusion, the results suggest that leftward attentional bias is not the cause of the VEP asymmetry.

Regarding the findings of larger ipsilateral than contralateral N1 amplitudes at the 1st serial position, we might speculate that initiation of attentional monitoring (looking for a target) may produce different effects on VEP amplitudes than attentional selection of a target, which typically enhances VEPs evoked by selected targets (Eimer, 2014). If this were true, however, the effect should be observed for all stimuli preceding targets. Interestingly, recent findings by Slagter, Prinssen, Reteig, and Mazaheri (2016) suggest that continuous attending to one VF enhances P1 amplitudes pre-

dominantly at ipsilateral sites, which supposedly reflects inhibition of irrelevant sources of information (cf. Klimesch, 2011), whereas N1 amplitudes are enhanced predominantly at contralateral sites, reflecting facilitation of target discrimination. In line with such reasoning, the present result might reflect suppression of the latter process at the 1st serial position of the RSVP stream, because targets never occurred at the 1st position. However, it is difficult to draw any conclusion from comparisons of our Experiment 2 and Slagter et al.'s (2016) study. Most notably, they reported only effects for target stimuli whereas we have analyzed effects for non-target stimuli, and their procedure comprised only single VF stimulation without any competition between VFs, in contrast to bilateral RSVP that entails a strong competition.

4.5. Specialization hypothesis

According to specialization hypothesis, Latin letters should evoke earlier and larger VEPs at the RH than the LH, while Tibetan letters should not, and Arabic digits should evoke earlier and larger VEPs at the LH (considering the recent results by Park et al., 2012, 2014; see also Shum et al., 2013). This hypothesis received least support in the results, since shorter latencies and larger amplitudes at the RH were found with all three stimulus types used in Experiment 1. Therefore, the VEP asymmetry does not seem to reflect hemispheric specializations in processing particular stimulus types. Possibly, the lateralization of perceptual processing attenuated or obscured those asymmetries. As mentioned in the Introduction, when perceptual demands are high, a LVF/RH advantage is often observed even in tasks that are otherwise performed better by the LH.

4.6. Further considerations on the RH advantage in perceptual processing

In conclusion, the most parsimonious explanation of the present results is that the RH advantage in early perceptual processing is the primary cause of the VEP asymmetry, whereas lateralization of familiarity processing, spatial attention, and possibly other factors like spatial frequency processing, reading, etc. (cf. Gazzaniga, 2000; Hellige, Laeng, & Michimata, 2010) may further modulate this asymmetry.

This RH advantage in early perceptual processing has been assumed to be a rather basic, domain-general, and plausibly “hard-wired” feature that makes RH better equipped to perform early operations on visual information (Grabowska & Nowicka, 1996; Hellige & Webster, 1979). The postulated “hard-wiring” may result from some hemispheric differences in microstructural features (like number and density of neurons in visual areas, and cytoarchitectonic differences), and/or macroscopic features (like volumes and cortical thickness) of particular areas of the visual system (Amunts, 2010; Chance, 2014). For instance, in a combined MRI and PET study with a large sample of healthy right-handed participants, Murphy, DeCarli, & McIntosh (1996) found that the striate cortex had on average significantly larger volume in the RH than in the LH. Alternatively, the VEP asymmetry might have mainly a functional character, reflecting, e.g., higher sensitivity of the right visual areas for information that is more useful at the initial stages of encoding not-yet-recognized stimuli, or just higher efficiency in extracting relevant visual features when stimulus visibility is not optimal (Gazzaniga, 2000; Grabowska & Nowicka, 1996; Hellige & Webster, 1979). Accordingly, this RH advantage might develop in a manner similar to the lateralization of reading. In case of reading, both hemispheres are exposed to the same stimulation during development, but the LH learns more than the RH (due to, e.g., specific anatomy or direct connections with language areas, cf. Dehaene & Cohen, 2011). In case of early perceptual pro-

cessing, the RH might be better equipped for the task. Thus, while both hemispheres are improving in the course of practice, the RH may acquire higher efficiency than the LH.

Regardless of its being a “hardware” or “software” feature (although these alternatives are not mutually exclusive) this asymmetry might be a significant part of the well-known overall RH dominance in many aspects of visuo-spatial cognition (Gazzaniga, 2000; Hellige et al., 2010). Also, the RH advantage in processing speed might contribute to lateralization of interhemispheric communication, i.e., faster information transfer from RH to LH than from LH to RH (Barnett & Corballis, 2005; Marzi, Bisiacchi, & Nicoletti, 1991; Siman-Tov et al., 2007). This would be in line with the so-called *horse-race* hypothesis, according to which a stimulus-response transmission in response time tasks is carried out through the shortest and quickest processing circuits (Marzi, 2010).

An interesting point to discuss is whether these early VEPs relate to conscious perception. In light of so called two-stage models of perception (e.g., Chun & Potter, 1995; Treisman & Gelade, 1980; Vogel, Luck, & Shapiro, 1998) early cortical processing occurs at the pre-selection or pre-attentive stage, which allows for only rapid and global processing that is possibly not related to the actual awareness of stimuli. There is, however, some disagreement in the consciousness literature in this matter. Some authors suggest that consciousness arises gradually and the early processing is enough for basic phenomenal consciousness (Lamme, 2010) or a crude “gist” perception of the whole scene to occur (Crick & Koch, 2003). Others claim that conscious perception arises only at the second stage of processing, after attentional selection and memory consolidation in the global neuronal workspace (Dehaene & Changeux, 2011) or higher-order systems (Lau & Rosenthal, 2011). We can speculate that the first of these two notions seems to be more applicable here, because these RSVP streams are actively and successfully monitored in search for targets, and this monitoring seems to require awareness of at least the gist of the stimuli, but certainly more evidence is needed for this hypothesis (see also Anzulewicz et al., 2015; Asplund, Fougner, Zughni, Martin, & Marois, 2014; Wierzbuch, Paulewicz, Asanowicz, Timmermans, & Cleeremans, 2014).

4.7. Methodological issue

In Experiment 1, both T1-correct and T1-incorrect trials were included in analysis, as in the previous RSVP studies reporting the VEP asymmetry (Verleger et al., 2011, 2013). It may be argued that, for better comparability of Experiments 1 and 2, the same criteria should have been applied for data selection, excluding trials with incorrectly reported T1 not only from Experiment 2 (13% on average, cf. Appendix) but also from Experiment 1 (14%). As mentioned in Methods, we changed the criterion in Experiment 2, because failure in reporting T1 may reflect failure in focusing attention on the target stream according to instructions. In contrast, in Experiment 1, failure in reporting T1 constituted a less specific mistake. Moreover, the increased error rate for Tibetan letters as distractors and T1 (18%, vs. 11% with Latin letters) did not necessarily mean that participants paid less attention in the Tibetan-letter group than in the Latin-letter group: Their task simply was more difficult, which, according to Lavie (2010), may even increase participants' attention. Thus, not being cleaned from incorrect-T1 trials, data from Experiment 1 might include some unspecific noise from unattended trials. Yet it seems plausible to assume that the main result of Experiment 1 (smaller VEP asymmetry with Tibetan letters than with letters or digits) is not due to such unspecific noise.

4.8. Summary

The present study investigates an asymmetry of the VEPs evoked by non-target stimuli in a bilateral RSVP task. Although modulated by stimulus familiarity and changed in extent by additive effects of attentional bias, the asymmetry remained present in each condition of the two experiments. Therefore, neither familiarity nor attentional bias seems to be the primary cause of the VEP asymmetry and the effect may be most parsimoniously explained by the hypothesis of a RH advantage at early cortical stages of perceptual processing.

Acknowledgments

This work was supported by Grant VE110/15-1/2 awarded from the Deutsche Forschungsgemeinschaft to R.V. as part of the network PAK270 “Neuro-cognitive mechanisms of conscious and unconscious visual perception”, and by Grant 2012/05/D/H56/03363 awarded from the National Science Centre of Poland to D.A. The authors thank Friderike Möller for her contribution in data collection.

Appendix A. Behavioral data: accuracy of target identification

A.1. Experiment 1

A.1.1. Data analysis

Percentages of correctly identified T1 were calculated from all trials, and percentages of correctly identified T2 were computed from all correctly identified T1 trials. These accuracy rates were analyzed by means of ANOVAs with Visual Field (LVF, RVF), Side Change (T1 and T2 at the same side, or different sides) and Lag (1, 3, 5) as within-subject factors, and Stimulus Type (Latin letters, Arabic digits, Tibetan letters) as between-subject factor.

Pearson's correlation coefficients were calculated to analyze correlations between visual field asymmetry indices of behavioral identification of T1 and T2 (calculated as LVF-RVF) and hemispheric asymmetry indices of distractor-evoked VEPs (cross correlation data, maxima of PO8-PO7 difference, and VEP amplitudes and latencies: PO7 was subtracted from PO8 for amplitude analyses and PO8 was subtracted from PO7 for latency analyses, to have positive values in each analysis). These VEP asymmetry indices were calculated from data averaged across the five serial positions (we also analyzed the correlations for each serial position separately, but the results were very similar).

A.1.2. Results

Mean T1 and T2 identification rates for each condition are presented in Table 1. T2 identification rates are additionally presented in Fig. 8.

A.1.2.1. T1 identification. The overall identification rate was 86% (SD = 7%). Accuracy slightly varied across the three Stimulus Types (of both distractors and T1), $F_{2,52} = 5.8$, $p = 0.005$, being highest for Latin letters (89%), intermediate for Arabic digits (86%), and lowest for Tibetan letters (82%). (Latin vs. Tibetan letters: $F_{1,35} = 10.5$, $p = 0.003$; Latin letters vs. Digits: $F_{1,33} = 3.4$, $p = 0.075$; digits vs. Tibetan letters: $F_{1,35} = 2.6$, $p = 0.11$.) The main effect of Visual Field and its interaction with Stimulus Type were not significant, $F_s < 1.0$.

A.1.2.2. T2 identification. T2 was identified with 77% accuracy. The main effects of Side Change, $F_{1,52} = 159.5$, $p < 0.001$, and Lag,

Table 1
Percentages of correct T1 and T2 identification in Experiment 1.

Lag	T1–T2 Side	Visual Field	Distractors	T1 Mean% (SD)	T2 Mean% (SD)
Lag 1	Same	LVF	Latin	88 (7)	95 (8)
			Tibetan	71 (14)	85 (14)
			Digits	89 (6)	98 (2)
		RVF	Latin	88 (7)	93 (10)
			Tibetan	76 (11)	84 (13)
			Digits	89 (6)	98 (3)
	Different	LVF	Latin	87 (7)	74 (21)
			Tibetan	83 (11)	46 (19)
			Digits	84 (8)	73 (19)
		RVF	Latin	87 (8)	54 (18)
			Tibetan	84 (8)	33 (12)
			Digits	83 (8)	70 (17)
Lag 3	Same	LVF	Latin	89 (10)	85 (14)
			Tibetan	84 (8)	77 (16)
			Digits	84 (9)	92 (9)
		RVF	Latin	91 (6)	75 (16)
			Tibetan	86 (9)	67 (19)
			Digits	85 (8)	91 (8)
	Different	LVF	Latin	91 (7)	88 (17)
			Tibetan	86 (8)	66 (22)
			Digits	86 (7)	85 (15)
		RVF	Latin	90 (8)	76 (17)
			Tibetan	83 (7)	53 (19)
			Digits	85 (6)	81 (14)
Lag 5	Same	LVF	Latin	90 (9)	88 (12)
			Tibetan	84 (6)	79 (16)
			Digits	86 (10)	92 (6)
		RVF	Latin	90 (7)	75 (17)
			Tibetan	83 (10)	72 (16)
			Digits	88 (8)	87 (8)
	Different	LVF	Latin	93 (6)	88 (12)
			Tibetan	84 (9)	77 (15)
			Digits	87 (7)	89 (8)
		RVF	Latin	90 (7)	80 (13)
			Tibetan	84 (7)	66 (18)
			Digits	86 (8)	84 (11)

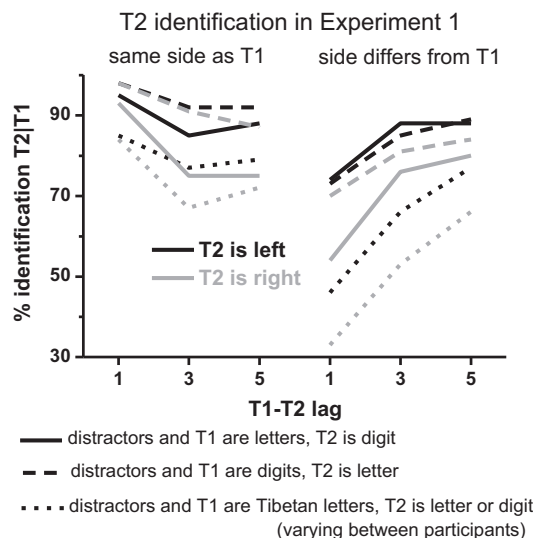


Fig. 8. (Appendix A) Mean identification rates of T2 in Experiment 1.

and lag 5 (82%), whereas in the different-side condition accuracy was lowest at lag 1 (58%) and increased at lag 3 (75%) and lag 5 (81%). As with T1, T2 identification rates varied across the three Stimulus Types, $F_{2,52} = 16.2$, $p < 0.001$. They were lowest when distractors and T1 were Tibetan letters (with T2 being either digits or Latin letters, 67%), were highest when distractors and T1 were Arabic-digits (with T2 being Latin letters, 87%), and intermediate when distractors and T1 were Latin letters (with T2 being digits, 81%) (Latin vs. Tibetan distractors: $F_{1,35} = 10.9$, $p = 0.002$; Latin letter vs. digit distractors: $F_{1,33} = 3.3$, $p = 0.078$; Digit vs. Tibetan distractors: $F_{1,35} = 30.4$, $p < 0.001$). Stimulus Type interacted with Lag, $F_{4,104} = 2.7$, $p = 0.04$, reflecting a larger increase in T2 accuracy from lag 1 to lag 5 after Tibetan distractors and T1 (12%) than with Latin (4%) and digit (4%) distractors and T1.

As usual, a LVF advantage in T2 identification was observed (LVF: 82% vs. RVF: 74%), $F_{1,52} = 47.7$, $p < 0.001$, that was modified, as usual, by an interaction between Visual Field, Side Change and Lag, $F_{2,104} = 8.3$, $p < 0.001$: At lag 1, the LVF advantage was significant only in the different side condition, $F_{1,52} = 29.1$, $p < 0.001$ (in the same side condition: $F = 1.5$, n.s.), whereas at the two longer lags there was no interaction between Visual Field, Lag, and Side Change, $F_{1,52} = 1.4$, n.s., while the LVF advantage remained significant, $F_{1,52} = 30.8$, $p < 0.001$. Of interest, the interaction Visual Field \times Stimulus Type was significant, $F_{2,52} = 4.4$, $p < 0.02$, reflecting a smaller Visual Field effect when distractors and T1 were Arabic digits (and T2 were letters). This might be due to a ceiling effect in T2 identification in the LVF with Arabic digits (dashed lines in Fig. 8).

A.1.2.3. Correlations between VEP asymmetry and target identification rates. No significant correlations were found between the VEP asymmetry indices and the visual field asymmetry indices of T1 ($r \leq 0.08$, n.s.) and T2 identification ($r \leq -0.23$, $p \geq 0.11$, see Fig. 9).

A.1.2.4. Summary. Experiment 1 provided typical and repeatedly replicated results, especially in terms of the LVF advantage in T2 identification (Asanowicz et al., 2013; Holländer et al., 2005; Verleger et al., 2009; Verleger et al., 2011; Verleger et al., 2013; Śmigajewicz et al., 2010).

A.2. Experiment 2

A.2.1. Data analysis

T1 and T2 identification rates were calculated in the same way as in E1. The data were analyzed by means of ANOVAs with Visual Field (LVF, RVF) and Lag (2, 4, 6, 8) as within-subject factors. Mean T1 and T2 identification rates for each condition are presented in Table 2.

A.2.2. Results

A.2.2.1. T1. identification. The overall T1 identification rate was 87% (SD = 13%). Only the main effect of Visual Field was significant, $F_{1,19} = 6.6$, $p = 0.02$, showing 3% of RVF advantage (cf. Śmigajewicz et al., 2010).

A.2.2.2. T2. identification. T2 was identified with 84% accuracy (SD = 14%). The main effect of Lag was significant, $F_{3,57} = 25.8$, $p < 0.001$, showing the typical attentional blink effect (accuracy from lag 2 to 8: 71%, 81%, 91%, 93%, respectively). In contrast to our 'standard' bilateral RSVP task (Exp.1, Verleger et al., 2011), here, neither the main effect of Visual Field, $F_{1,19} = 3.5$, $p = 0.20$, nor the Lag \times Visual Field interaction, $F < 1.0$, n.s., were significant.

$F_{2,104} = 12.7$, $p < 0.001$, and a Side Change \times Lag interaction, $F_{2,104} = 222.8$, $p < 0.001$, showed that in the same-side condition accuracy was highest at lag 1 (92%) and decreased at lag 3 (81%)

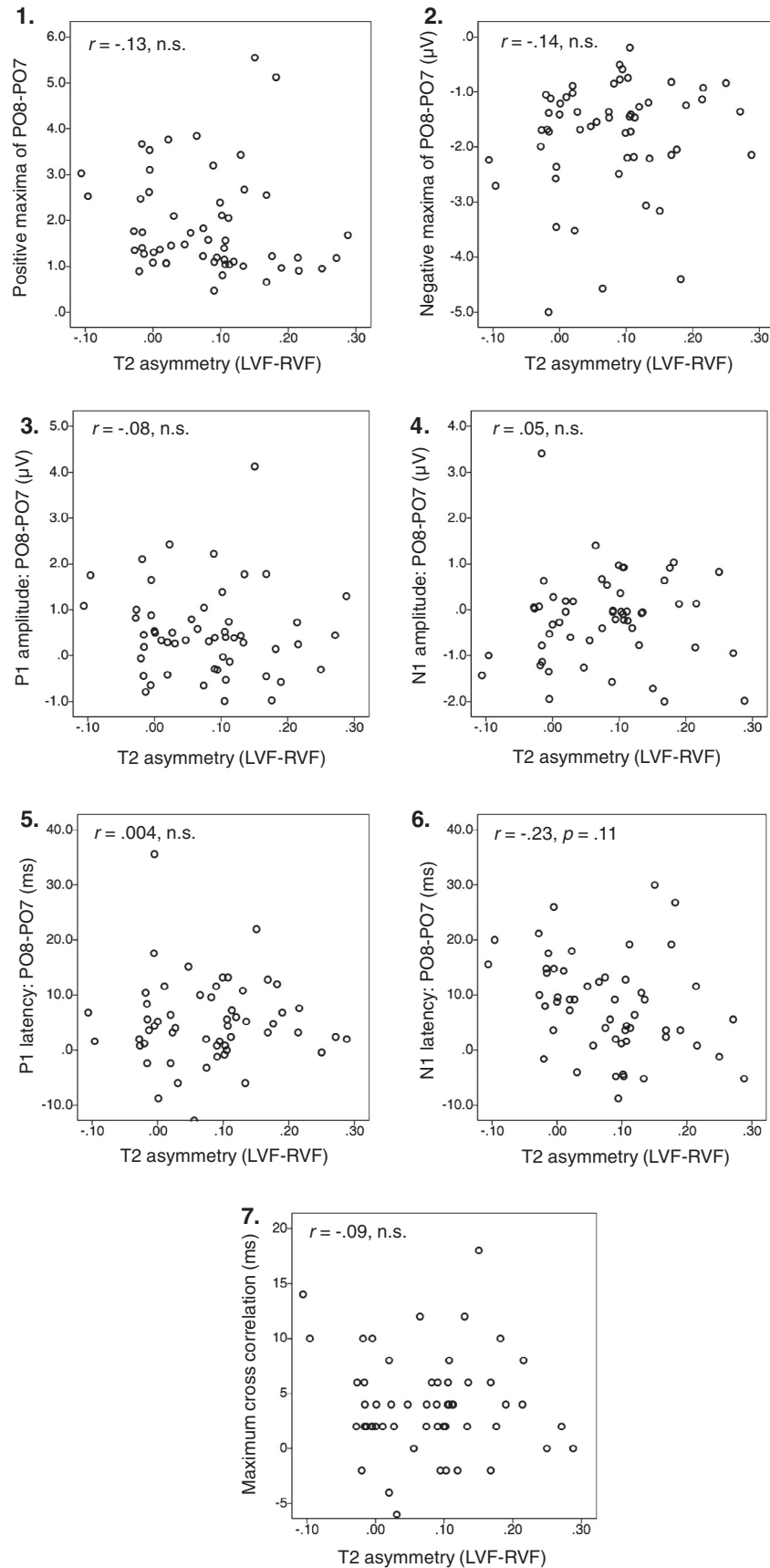


Fig. 9. (Appendix A) Experiment 1. Scatterplots for correlations between visual-field asymmetry indices of T2 identification (calculated as LVF-RVF, thus positive values indicate LVF advantage) and hemispheric asymmetry indices of distractor-evoked VEPs: maxima of PO8-PO7 difference (panel 1 and 2), VEP amplitudes and latencies (PO7 was subtracted from PO8 for amplitude analyses, panel 3 and 4, and PO8 was subtracted from PO7 for latency analyses, panel 5 and 6), and cross correlation data (panel 7).

Table 2
Percentages of correct T1 and T2 identification in Experiment 2.

Lag	Visual field	T1 Mean% (SD)	T2 Mean% (SD)
Lag 2	LVF	85 (13)	73 (17)
	RVF	88 (13)	70 (23)
Lag 4	LVF	85 (15)	82 (16)
	RVF	88 (12)	80 (21)
Lag 6	LVF	86 (13)	93 (8)
	RVF	89 (11)	89 (11)
Lag 8	LVF	85 (14)	95 (9)
	RVF	87 (14)	92 (9)

The behavioral data of E2, along with the target-evoked ERPs, will be reported in details and discussed elsewhere (Asanowicz, Kruse, Śmigasiewicz & Verleger, in preparation).

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